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# Arnel R. Hallauer: An appreciation

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**Abstract**
This volume is dedicated to Arnel R. Hallauer. For the last 3 decades, he has made significant contributions to quantitative genetics with particular reference to corn breeding. His research effort has focused on the evaluation of quantitative genetic theory, and the evaluation and utilization of recurrent selection for population improvement and the efficient development of new inbred lines for use in corn hybrids.

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# ARNEL R. HALLAUER

**An appreciation**
**by G.F. Sprague[1] and K.R. Lamkey[2]**

This volume is dedicated to Arnel R. Hallauer. For the last 3 decades, he has made significant contributions to quantitative genetics with particular reference to corn breeding. His research effort has focused on the evaluation of quantitative genetic theory, and the evaluation and utilization of recurrent selection for population improvement and the efficient development of new inbred lines for use in corn hybrids.

ARNEL R. HALLAUER

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## Biographical Sketch

Arnel R. Hallauer is a midwesterner. He was born in Kansas on May 4, 1932 at Netawaka. His interest in corn research began when he was 14, in the fall of 1946, when he had a part-time job with Dr. Lloyd A. Tatum harvesting experimental corn trials in Northeast Kansas. He continued working part-time with Dr. Tatum while attending high school (1946-1950), planting experimental corn trials in the spring and harvesting them in the fall. During the summer months of his high school years, he detasseled corn for the production of double-cross hybrid seed for Mr. Carl Overly of the Kansas Crop Improvement Association. These associations with Dr. Tatum and Mr. Overly led him to Kansas State University where he received his

B.S. degree with honors in 1954 with a major in Plant Science. During his undergraduate studies, he was continuously employed part-time on a hourly basis with the cooperative Federal-State corn breeding project at Kansas State University directed by Dr. Tatum. During this time in his undergraduate studies, he experienced all aspects of the breeding project including preparing seed, planting, data collection, harvesting, pollinating in the breeding nurseries, and analyzing and summarizing data of experimental trials.

After finishing his undergraduate degree, followed by 2 years of military service (1954-1956), Dr. Tatum impressed with his young assistant's dedication and work ethic urged Arnel to attend graduate school for an advanced degree in plant breeding. After considering offers from several universities, Iowa State University became his choice. This offer was chosen after consultation with Dr. Tatum, because the offer included working with Dr. George F. Sprague, a plant breeder who was highly regarded for his research program. Dr. Hallauer completed the requirements for the M.S. degree in plant breeding in 1958. He accepted a position as a research agronomist with the U. S. Department of Agriculture, Agriculture Research Service (USDA, ARS) in the summer of 1958. The major responsibilities of this position were conducting host-plant resistance studies with Mr. Ferd Dicke at the USDA, ARS corn insects laboratory in Ankeny, Iowa. While working for the USDA, ARS, he continued on in graduate school and received his Ph.D. in 1960. Dr. W.A. Russell served as his major advisor for the Ph.D. degree after Dr. Sprague was transferred to Beltsville, Maryland in 1958 to become USDA, ARS Investigations Leader for corn and sorghum research.

With the completion of his Ph.D. degree he was transferred to North Carolina State College as a USDA,ARS Post-Doctoral Research Geneticist to spend a year with Professor C. Clark Cockerham. In 1962, he was transferred back to Ames as a USDA,ARS Research Geneticist, where he continued in this capacity for the next 27 years. In December of 1989, Dr. Hallauer retired from the USDA,ARS and accepted a position with Iowa State University as Professor of Plant Breeding. In 1991, he was promoted to C. F. Curtiss Distinguished Professor in Agriculture. The research interests throughout his career have been in the extension and evaluation of quantitative genetic theory as it relates to corn breeding. Before detailing his accomplishments, it is necessary to put the development of corn breeding and quantitative genetic theory in historical perspective.

**Quantitative Genetics: A Historical Perspective**

With the beginning of the modern era of corn breeding (1920-1950), hybrids rapidly supplanted the previously grown open-pollinated varieties. In the major corn producing states, this transition was completed in about 10 years with an accompanying substantial increase in per acre yields. Following this initial success, corn breeders continued their sampling of open-pollinated varieties but to an increasing extent devoted their efforts to "second-cycle" breeding; the development of new lines from the best parents of the then current hybrids. When such lines began to reach the evaluation stage, the results were generally disappointing. The newer lines tended to be higher yielding than their original parents but the hybrids among them were not markedly superior to those first released (HALLAUER, 1990).

During this period (1920-1950), some corn breeders interpreted this experience as indicating that the big gains had been achieved and that further progress would be limited and difficult to achieve. Others interpreted the results as indicating a conceptual limitation of the methods in use and directed their efforts toward the development and evaluation of new concepts and procedures. Such was the beginning of quantitative genetics as applied to corn breeding.

**Era: Quantitative Genetics Integrated into Corn Breeding**

The quantitative genetics approach was not universally accepted. Reservations as to the utility of the method were due, in large part, to the perception that the mathematical restrictions of the model might limit its biological utility. The assumptions of the model causing most concern were: no mutation, no linkage, and no epistasis. These restrictions were imposed to simplify algebraic manipulations rather than the belief that such phenomena either did not exist or were of limited importance. Classical genetics had devoted considerable effort in detailed studies of precisely these topics.

New mutations would be expected to have only minor effects in the development of stable lines but could be of importance in long term selection experiments or synthetic populations developed by the breeders. The effects of linkage bias would be minimized if quantitative traits were conditioned by large numbers of genes with random genomic distribution. Where linkage equilibrium can be assumed, linkage bias would be minimized but unfortunately for many populations used, $F_2$'s, backcrosses, etc., linkage bias would be at a maximum. The failure to accommoda-

FIGURE 1 - Corn breeding project ca 1952. From left to right, Bob Ward (hourly), Michelsen (technician), Dr. W.A. Russell, Dr. L.H. Penney, Dr. G.F. Sprague, Dr. A.R. Hallauer, Angus Hyer (graduate student), Rosbacco (visiting scientist) S.L. Marvick (technician), Pedro Reyes (graduate student), Mohammad Khan (graduate student).

te epistasis also could introduce a bias. Epistasis had been well established in classical genetic studies. Presumably it might be equally important for quantitative traits though this had yet to be established.

With the limitations arising from these and other sources the question remained: Did the mathematical models *encompass* sufficient detail to provide a useful picture of the biological complexites involved? More specifically would the models provide estimates of population parameters which would be useful for predicting response to selection or for comparing relative efficiency of alternative breeding systems? Answers to such questions could come only from detailed experiments. This was the situation when Dr. Hallauer entered the field and his career has been devoted to seeking answers to these and related questions.

Obviously the relative importance of different types of gene action (additive, dominance, epistatic) involved in the inheritance of quantitative traits was of prime importance. Dr. Hallauer has contributed greatly to undestanding gene action in corn through a

FIGURE 2 - Meeting of the Chinese Academy of Science, ca 1987. From left to right, Su Guo Qun, Professor Li, Dr. A.R. Hallauer, and Ren Rui.

variety of experimental approaches, some of which will be discussed briefly in the sections which follow.

**Hallauer's Contributions**

He conducted an extensive study relating mean performance for a series of quantitative traits to decrease in heterozygosity achieved under three systems of inbreeding; self-fertilization, half and full-sib matings. The differences in rates of approach to homozygosity were found to be of limited importance. For most of the traits studied, the linear regression relating mean performance and level of inbreeding accounted for 98-99% of the variation. This would be the expectation with independent loci and any degree of dominance. Departures from linearity would be evidence for epistasis. The quadratic component for the trait, yield, was highly significant but accounted for only 0.5% of the total variation for yield (HALLAUER and SEARS,1973; GOOD and HALLAUER, 1977).

In quantitative genetics, epistasis is measured by the nonadditivity of effects among loci. This nonlinearity could arise from additive x additive, additive x dominance or dominant x dominant interactions. Several methods have been used for the estimation of epistasis.

Using a series of random lines derived from the corn population Iowa Stiff Stalk Synthetic (BSSS), Dr. Hallauer conducted both North Carolina Design I and Design II studies to obtain variances for the additive (A) and dominance (D) components and the three epistatic components (AA), (AD), and (DD). The additive component accounted for 93% of the total genetic variance for yield. When dominance was included, the two accounted for 99%. Thus epistasis, as measured, was a minor contributor to the genetic variance for yield (SILVA and HALLAUER, 1975).

On the possibility that epistasis might vary with the level of performance of the parental lines, four groups of lines were chosen: first cycle, second cycle, good, and poor. Within each set, all possible $F_1$ hybrids were obtained and, through selfing and backcrossing heterozygosity levels of 0, 25, 50, and 100% were established within each set. Evidence for epistasis was examined by using departures from linearity in the regression of perfomrance on heterozygosity. Evidence for epistasis was greatest among the "poor" set but was relatively unimportant for most traits measured within each group. Thus evidence for epistasis exists but this type of gene action appears to be relatively unimportant with the methods of estimation currently available (MARTIN and HALLAUER, 1976).

The quantitative genetic approach has proven very useful in providing theoretical expectations for improvement from selection under alternative breeding systems. Corn breeders throughout the world have benefited from Dr. Hallauer's book. Here, he has performed a great service in preparing a detailed survey of his own studies and the extensive work of others as it relates to those expectations in his excellent book that he co-authored with J.B. Miranda, Filho entitled *Quantitative Genetics and Maize Breeding*. The breeding systems covered range from mass selection, selection within and among inbred families through the various modifications of recurrent selection. All of these systems are cyclical with the primary distinctions being the type of progenies evaluated and the time required to complete a cycle of selection.

Recurrent selection studies, with selection pressure primarily applied for yield, have been conducted with populations of differing genetic backgrounds; synthetics, composites and open-pollinated varieties. Response to selection is a function of allelic frequency and genetic variability as well as the selection pressure applied. Because there is no easy method for the estimation of allelic frequencies conditioning a quantitative trait, evaluation of response to selection has relied on changes in means and other population parameters over cycles of selection.

Estimates of additive ($\sigma^2_A$) and dominance ($\sigma^2_D$) variance provided a measure of the contribution of these types of gene action to genetic variability; these types of gene action being those most responsive to selection. Results from a number of studies, for all traits measured, indicated that $\sigma^2_A$ was consistently greater than $\sigma^2_D$, which was often zero or negative.

With these general findings as a background, genetic expectations were developed for a series of alternative breeding systems. These differ in cycle time and the precision of estimates may be influenced by replication over locations and years. Dr. Hallauer emphasized that each method might have relevance in a breeding program depending on the objective to be achieved.

Dr. Hallauer is well known for his ability to investigate, interpret, and relate quantitative genetics to efficient development of germplasm populations, inbred lines, and hybrids of corn. He developed the reciprocal full-sib selection (FR) method to combine recurrent selection procedures for population improvement with inbred and hybrid development (HALLAUER and EBERHART, 1970). Experiments have been designed to evaluate the actual genetic improvement that could be realized by this procedure. He initiated FR selection in 1963 in two prolific corn populations, BS10 and BS11. Eight cycles of selection have been completed and evaluated for direct [BS10(FR)Cn x BS11(FR)Cn] and indirect [BS10(FR)Cn and BS11(FR)Cn per se] response. The eight cycles of selection were effective for increasing grain yield of the population cross (6.5% per cycle), BS10 (2.9% per cycle) and BS11 (1.6% per cycle). These experiments have demonstrated that FR selection can be used effectively to improve populations and develop improved inbred lines simultaneously. The results from these experiments, along with data from other experiments that he has conducted, have also shown that inbred lines can serve effectively as testers in the development of corn hybrids. Most corn breeders in both the public and private sector have adopted the use of inbred testers in their breeding programs.

The Iowa corn breeding program has been characterized by one unique feature, quantitative genetic theory has been evaluated at two levels; by changes in population parameters as they are modified by the recurrent selection system imposed and by an independent evaluation of their applied utility. The lines chosen to form each new cycle are routinely evaluated for their possible commercial utility. The well known and highly utilized lines B14, B37, B73, and B84 were identified under this system. In a survey of the parentage of seed available for 1980 plantings, these four lines were involved in 19% of the total US seed supply (ZUBER and DARRAH, 1980). Publicly released recovered strains of these lines accounted for another 15%. The total use, 34%, may be an underestimate of the total usage of these germplasm sources because proprietary modified versions of these lines would not have been included in the survey. Impressive as these survey results are they represent usage for only a single year, whereas, these lines developed out of the cooperative Federal-State Iowa corn breeding program have been in use for a number of years. Thus, the cumulative contribution of these lines to U.S. and world maize production has been tremendous.

Dr. Hallauer's primary contributions to agriculture have occurred, directly and indirectly, because of his research in corn breeding. He has had a leading or supportive role in the development and evaluation of more than 30 corn synthetics and 18 inbred lines that have been released to the seed industry by the Iowa Agricultural Experiment Station during his years as leader of the Federal-State corn breeding research project. A survey sponsored by the American Seed Trade Association in 1980 showed that inbred B73 was used more extensively than any other inbred line in the production of hybrids in the U.S. B73 is also used widely as a parental line for hybrids in several European countries and Asia. The corn synthetics and inbred lines are also used by private company breeders in the development of new inbred lines. Corn breeders in the private sector frequently seek his counsel relative to breeding methods and the application of quantitative genetic theories to breeding procedures. Several of his graduate students are now employees in the seed industry where they are engaged in the development of improved corn hybrids for agriculture in Iowa and the U.S.

Recurrent selection has been used effectively by Dr. Hallauer as a procedure for integrating exotic germplasm into existing breeding programs. He showed that recurrent phenotypic selection for maturity and plant type was effective for adapting foreign germplasm to U.S. Corn Belt environments (HALLAUER and SEARS, 1972). He has successfully adapted Latin American cultivars Eto Composite, Tuxpeno, and Antigua, and is currently working with Suwan 1 from southeast Asia, Mexican Dent, and Cateto x Carribean Flint. These populations are used extensively in the tropics. The improved germplasm has good yield potential and a greater frequency of individuals with disease and insect resistance compared with populations used for the development of current commercial hybrids. His concern with genetic vulnerability and interest in the use of exotic germplasm has led to the development of a germplasm research position in the USDA,ARS corn research project at Iowa State University.

In addition to his exemplary research career, Dr. Hallauer has also been an outstanding educator. He has devoted much attention to the training of graduate students who have come from the U.S. and 16 foreign countries. He has been major advisor to 47 students (16 M.S. and 31 Ph.D.) and 12 postdoctoral or visiting scientists. Currently he serves as major advisor for 13 students (2 M.S. and 11 Ph.D.). Additionally, he has served on the graduate study committee for over 95 students in plant breeding and related sciences. Many foreign scientists have spent varying periods of time with him to observe and discuss his research studies in maize breeding. He currently teaches one graduate level course in plant breeding.

Dr. Hallauer has received numerous honors and awards in recognition of his research contributions. Among these are: Fellow (American Society of Agronomy, 1979), Fellow, (Crop Science of America Society, 1985), Crop Science Award (Crop Science of

America Society, 1981), Agronomic Achievement Award-Crops (Agronomy Society of America, 1989), Applied Research and Extension Award (Iowa State University, 1981), Distinguished Fellow Award (Iowa Academy of Sciences, 1985), Northrup King Recognition Award for Research in Corn Breeding (1985), Breeding and Genetics Award (National Council of Commercial Plant Breeders, 1984), Scientist of the Year Award (U. S. Department of Agriculture, 1985), Iowa Govenor's Science Application Medal (1990), member of the National Academy of Sciences (1989), and DeKalb Crop Science Distinguished Career Award (Crop Science Society of America, 1990).

Due, in large measure, to Dr. Hallauer's research activities Plant Breeding is now firmly based on quantitative genetic principles and given a knowledge of population parameters prediction can be made as to the relative effectiveness of alternative breeding systems. The impact of his research on corn breeding and production has been enormous. We find it both a pleasure and an honor to participate in honoring Dr. Arnel R. Hallauer for his brilliant and innovative contributions to corn breeding. The assemblage of papers in this volume is a testimony to this.

## REFERENCES

Good R.L., A.R. Hallauer, 1977 Inbreeding depression in maize by selfing and full-sibbing. Crop Sci. **17:** 935-940.

Hallauer A.R., 1990 Methods used in developing maize inbreds. Maydica **35:** 1-16.

Hallauer A.R., S.A. Eberhart, 1970 Reciprocal full-sib selection. Crop Sci. **10:** 315-316.

Hallauer A.R., J.B. Miranda Fo, 1988 Quantitative Genetics in Maize Breeding. 2nd ed. Iowa State Univ. Press, Ames, IA.

Hallauer A.R., J.H. Sears, 1972 Integrating exotic germplasm into Corn Belt maize breeding programs. Crop Sci. **12:** 203-206.

Hallauer A.R., J.H. Sears, 1973 Changes in quantitative traits associated with inbreeding in a synthetic variety of maize. Crop Sci. **13:** 327-330.

Martin J.M., A.R. Hallauer, 1976 Relation between heterozygosis and yield for four types of maize inbred lines. Egypt. J. Genet. Cytol. **5:** 119-135.

Silva J.C., A.R. Hallauer, 1975 Estimation of epistatic variance in Iowa Stiff Stalk Synthetic maize. J. Hered. **66:** 290-296.

Zuber M.S., L.L. Darrah, 1980 1979 U.S. corn germplasm base. pp. 234-249. *In:* (ed. H.D. Loden and D. Wilkerson). Proceedings of the 35th Annual Corn and Sorghum Research Conference. Chicago, 9-11 December 1980. Washington, DC: American Seed Trade Association.